Liverpool Marine Biology Committee.

L.M.B.C. MEMOIRS

ON TYPICAL BRITISH MARINE PLANTS & ANIMALS

EDITED BY W. A. HERDMAN, D.Sc., F.R.S.

VI.

LEPEOPHTHEIRUS

AND

LERNÆA.

BY

ANDREW SCOTT,

Resident Fisheries Assistant at the Piel Hatchery.

(With 5 Plates)

PRICE TWO SHILLINGS.

LONDON
WILLIAMS & NORGATE
MARCH, 1901.

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NOTICE.

THE Committee desire to intimate that no copies of these Memoirs will be presented or exchanged, as the prices have been fixed so low that most of the copies will have to be sold to meet the cost of production.

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" IV. Codium—published in April, 1900, 26 pp. and three plates, price 1s. 6d.

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" VI. Lepeophtheirus and Lernæa—now ready (March, 1901), 62 pages and five plates, price 2s.

" VII. Lineus—(in April), with four plates.

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EDITOR'S PREFACE.

THE Liverpool Marine Biology Committee was constituted in 1886, with the object of investigating the Fauna and Flora of the Irish Sea.

The dredging, trawling, and other collecting expeditions organised by the Committee have been carried on intermittently since that time, and a considerable amount of material, both published and unpublished, has been accumulated. Fourteen Annual Reports of the Committee and five volumes dealing with the "Fauna and Flora" have been issued. At an early stage of the investigations it became evident that a Biological Station or Laboratory on the sea-shore nearer the usual collecting grounds than Liverpool would be a material assistance in the work. Consequently the Committee, in 1887, established the Puffin Island Biological Station on the North Coast of Anglesey, and later on, in 1892, moved to the more commodious and convenient Station at Port Erin in the centre of the rich collecting grounds of the south end of the Isle of Man.

In these thirteen years' experience of a Biological Station (five years at Puffin Island and eight at Port Erin), where College students and young amateurs formed a large proportion of the workers, the want has been constantly felt of a series of detailed descriptions of the structure of certain common typical animals and plants, chosen as representatives of their groups, and dealt with by specialists. The same want has probably been felt in other similar institutions and in many College laboratories.

The objects of the Committee and of the workers at the Biological Station have hitherto been chiefly faunistic and speciographic. The work must necessarily be so at first

when opening up a new district. Some of the workers have published papers on morphological points, or on embryology and observations on life-histories and habits; but the majority of the papers in the volumes on the "Fauna and Flora of Liverpool Bay" have been, as was intended from the first, occupied with the names and characteristics and distribution of the many different kinds of marine plants and animals in our district. And this faunistic work will still go on. It is far from finished, and the Committee hope in the future to add greatly to the records of the Fauna and Flora. But the papers in the present series are quite distinct from these previous publications in name, in treatment, and in purpose. They will be called the "L.M.B.C. Memoirs," each will treat of one type, and they will be issued separately as they are ready, and will be obtainable Memoir by Memoir as they appear, or later bound up in convenient volumes. It is hoped that such a series of special studies, written by those who are thoroughly familiar with the forms of which they treat, will be found of value by students of Biology in laboratories and in Marine Stations, and will be welcomed by many others working privately at Marine Natural History.

It is proposed that the forms selected should, as far as possible, be common L.M.B.C. (Irish Sea) animals and plants of which no adequate account already exists in the text-books. Probably most of the specialists who have taken part in the L.M.B.C. work in the past, will prepare accounts of one or more representatives of their groups. The following have already promised their services, and in many cases the Memoir is already far advanced. The first Memoir appeared in October and the second in December, 1899, the third in February, and the fourth in April, 1900, the fifth in January, 1901, and this sixth one

in March, while the seventh will be ready early in April; others will follow, it is hoped, in rapid succession.

Memoir I. ASCIDIA, W. A. Herdman, 60 pp., 5 Pls., 2s.
„ II. CARDIUM, J. Johnstone, 92 pp., 7 Pls., 2s. 6d
„ III. ECHINUS, H. C. Chadwick, 36 pp., 5 Pls., 2s.
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FUCUS, J. B. Farmer.
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PLAICE, F. J. Cole and J. Johnstone.
BOTRYLLOIDES, W. A. Herdman.
CUTTLE-FISH (ELEDONE), W. E. Hoyle.
OSTRACOD (CYTHERE), Andrew Scott.
PATELLA, J. R. A. Davis and H. J. Fleure.
CALANUS, I. C. Thompson.
ACTINIA, J. A. Clubb.
BUGULA, Laura R. Thornely.
HYDROID, E. T. Browne.
MYXINE, G. B. Howes.
BUCCINUM, M. F. Woodward.
CALCAREOUS SPONGE, R. Hanitsch.
ARENICOLA, J. H. Ashworth.
ANTEDON, H. C. Chadwick.
OYSTER, W. A. Herdman and J. T. Jenkins.
PORPOISE, A. M. Paterson.

In addition to these, other Memoirs will be arranged for, on suitable types, such as *Sagitta* (by Mr. Cole), a Cestode and a Turbellarian (by Mr. Shipley), *Carcinus*, an Amphipod, and a Pycnogonid (probably by Dr. A. R. Jackson).

As announced in the preface to ASCIDIA, a donation from Mr. F. H. Gossage of Woolton met the expense of preparing the plates in illustration of the first few Memoirs, and so enabled the Committee to commence the publication of the series sooner than would otherwise have been possible. A second donation received since from Mr. Gossage, and another recently from Mrs. Holt, are regarded by the Committee as a welcome encouragement, and will be a great help in carrying on the work.

W. A. HERDMAN.

University College, Liverpool,
March, 1901.

NOTE.—The present Memoir by Mr. Andrew Scott differs from those published and contemplated inasmuch as it deals with two generic types. At one time I thought of issuing LEPEOPHTHEIRUS and LERNÆA as separate Memoirs; but, on consideration, it seemed clear that these two diverse types of Epizoa supplemented one another and illustrated well the range in form of the parasitic Copepoda, and that consequently it would be convenient to the student to have them under one cover.—W.A.H.

L.M.B.C. MEMOIRS.

No. VI. LEPEOPHTHEIRUS AND LERNÆA.

BY

ANDREW SCOTT.

Introduction.

There are comparatively few fishes that do not, at some period of their life history, prove on careful examination to be the host of at least one kind of parasite, either crustacean or worm. The worm parasites are usually found infesting the alimentary canal (Nematodes and Cestodes), the gills and skin (Trematodes and Bdellodes), while Crustacean (Copepod) parasites are almost entirely confined to places in direct communication with the exterior, such as the skin itself, the fins, the mouth, the branchial chamber, attached to the gills and operculum, in the nostrils, and in the mucous canals. They may even be found attached to the eye, as *Lernœenicus sprattœ* in the sprat (*Clupea sprattus*); and *Lernœopoda elongata* in the Greenland Shark* (*Acanthorhinus carcharias*), causing in the latter at any rate partial blindness; or burrowing into the abdominal cavity, as *Penella exocœti* in the flying fish† (*Exocœtus volitans*), till only the ends of the ovisacs are visible from the exterior.

The Copepod fish parasites have attracted much attention from Zoologists for a very long period, since the time when Aristotle, in his "Historia Animalium," tells us that the tunny and the sword fish are tormented by a sort of worm which fastens itself under the fin. Many of

* Mr. R. L. Ascroft, of Lytham, who visited Iceland on a "steam liner," fishing for halibut, &c., a year or two ago, says nearly all the sharks caught on the lines had these parasites in their eyes.

† One was exhibited at a meeting of the Liverpool Biol. Soc. in 1897, infested by two such parasites, recorded as *P. blainvilli*, which in turn were covered with a number of small Cirripedes.—Trans. L'pool Biol. Soc. vol. xi., p. xii.

the parasites now known to be Copepods were not at first recognised as Crustacea, chiefly because of the difficulty of making out the true characters and the absence of knowledge as to the life-histories. There was much difference of opinion even as to which were really the anterior and posterior extremities of these animals, due to the fact that the posteriorly placed ovisacs of the then known forms are cylindrical tubes which were by some supposed to be the antennules, and therefore that end was called the anterior. Hence many of the drawings of the earlier authors represent the animals standing on their heads.

Baird's "British Entomostraca," published by the Ray Society in 1850, marks an important epoch in our knowledge. This author gives an interesting historical account of the group, brings together all that was previously known, and gives a very full account, with excellent figures, of all the British species known at that time, and although some of these are inaccurate in detail, or have been added to by more recent investigations, still Baird's monograph is indispensable to any one working at the subject. Since 1850 comparatively little has been done in this country to increase our knowledge regarding the distribution or habits of these crustaceans. Within the past few years, however, the study has revived and some important papers, mainly speciographic, have been published.

The latest classification of the Copepod fish parasites arranges them under seven families, as follows:—Ergasilidæ, Caligidæ, Dichelestidæ, Philichthyidæ, Lernæidæ, Chondracanthidæ, and Lernæopodidæ. With the exception of the Philichthyidæ, all these families have representatives living on fishes found in the seas around our coasts.

These parasites vary considerably in size, ranging from one-thirtieth of an inch to nearly two inches in length. They also differ very much in shape. Some have their locomotor organs well developed, and are capable when necessary of leading a pelagic life for a period. Others have lost all swimming power, and become mere inert sacs, securely attached to their host by anchor processes, embedded in the tissues, and when taken off their host they soon die from want of food and oxygen.

The sexes are separate, the males as a rule being much smaller than the females. In many cases the males are practically parasitic on the females, especially those of the Chondracanthidæ and Lernæopodidæ. The fact that the males are found upon egg-bearing females of the above families is due to their power of locomotion having been lost when they reached maturity. When once they have settled down and matured they are unable to change their position to any extent. Fertilisation of the female is effected early in its life history, before the metamorphosis is completed. One copulation, apparently, is all that is necessary to fertilise the female for life. The resulting embryos remain attached to the external opening of the oviducts, either in a single or multiserial column, enclosed in a sac, until they hatch. The period of incubation extends over several weeks. The young parasites hatch out as nauplii, with three pairs of appendages. The nauplii undergo metamorphosis, which in some forms after a certain stage is reached is retrogressive, finally leading to the adult condition.

The Copepod fish parasites are generally regarded as being composed of about sixteen somites. Usually, however, some of these somites are suppressed or fused together, forming one compound segment, the true character of which is rendered evident by the appendages

attached to it, each pair indicating a somite. At one end of the series, these parasites approach very nearly in structure and general appearance to the non-parasitic Copepods. At the other end they are extremely different, exhibiting most remarkable examples of retrograde development, and without a complete study of their life history it would be quite impossible to recognise them even as Crustacea.

In the following pages an account is given of the anatomy and metamorphosis of one member from each of the two very different families, the Caligidæ and the Lernæidæ, the forms chosen being *Lepeophtheirus pectoralis* and *Lernæa branchialis.*

The Caligidæ is the most extensive family of the Copepod fish parasites, and contains a larger number of genera and species than any of the others. As it stands at present, there are 124 species representing 25 genera. Three-fifths of the known species of Caligidæ belong to two genera, *Caligus* and *Lepeophtheirus.* Some earlier authors have not recognised the latter genus, and include the various species belonging to it in *Caligus.* There are, however, very important differences between the two which make their appearance early in life. These differences are constant, and give good cause for establishing a separate genus. *Caligus* has two semicircular suckers on the frontal margin of the cephalic shield, which are developed before the "chalimus"* stage is completed, and the biting part of the second maxillæ has only one tooth. In *Lepeophtheirus* these suckers are entirely absent all through life, and the biting part of the second maxillæ has two teeth. The changes that take place between the "nauplius" stage, when the animal is hatched from the

* The stage at which the animal first becomes attached to its host. (see p. 32).

egg, and the adult condition are practically the same in the two genera, and probably also in the other members of this family. From investigations carried on during the past two years, it may reasonably be concluded that *Lepeophtheirus*, throughout the remainder of its life and under normal conditions remains on the same fish that it attached itself to at the beginning of the "chalimus" stage. It is very rarely met with in tow-net collections. On the other hand, *Caligus* does not always remain on the same fish. At the completion of its "chalimus" stage it frequently leaves its host, and for a time leads a pelagic life. Tow-net collections often contain immature males and females, and occasionally mature males of *Caligus*, especially of *Caligus rapax*. Amongst these some may be found with a large notch in the middle of the frontal margin. This is due to the breaking of the chitinous filament by which they were secured to their host. The metamorphosis is a progressive one.

I.—LEPEOPHTHEIRUS (Müller).

This species was first described by O. F. Müller* under the name *Lernœa pectoralis*.

Mode of Occurrence.

Lepeophtheirus pectoralis is most frequently found upon the "white fluke" or flounder (*Pleuronectes flesus*). It also occurs on the plaice, dab, sole, &c. It does not confine itself to any particular part of the exterior. Males and immature forms of both sexes are to be found all over the skin on each side of the fish. Mature egg-bearing females, however, are usually found under the pectoral, the pelvic, the ventral and the dorsal fins. With careful

* Prodrom. Zoolog. Dan., 1776.

examination it is possible to collect a series of these parasites, from the early "chalimus" stage to the adult condition, from one fish. Sometimes only a few specimens occur on the fish. At other times large numbers are to be found. It is by no means rare to find between twenty and thirty mature females under each pectoral fin alone, as in the case which is illustrated in the cut. One hundred specimens of another species, *L. hippoglossi,* have been collected from the "white" side of a halibut in the Aberdeen Fish Market. The average length of a mature

Lepeophtheirus pectoralis, 32 specimens, on the pectoral fin of a Flounder from a photograph.

egg-bearing female is one-fifth of an inch, and of a male one-ninth of an inch. A mature female measures about one-tenth of an inch at its greatest breadth, and a male one-twelfth of an inch. These parasites attach themselves to the fish by means of their powerful second maxillipedes, assisted by the antennæ, and a decided pull has to be exerted before they can be torn away. By depressing the edges of the carapace and applying them closely to the skin, the parasite can increase its holding power to such an extent that the posterior end can be torn from the

anterior part without detaching it. The anterior part, when thus separated from the posterior, retains its vital powers for at least twenty-four hours. At first it swims about vigorously, but after some hours begins to get sluggish in its movements, and then finally dies. The posterior part does not live long when separated from the anterior. The parasites can be kept alive in sea water for upwards of six weeks after removal from the fish.

External Characters.

The animal is depressed dorso-ventrally, and is of a more or less oval shape, and distinctly divided into four parts (Plate I., fig. 1). The foremost one of these parts, and usually the largest, is almost circular in outline, and has all the appendages, with the exception of the fourth and fifth pairs of feet, attached to it. This part is known as the cephalo-thorax.

Viewed from above, this region is seen to be slightly convex and divided into four portions by imperfect sutures. Two of these sutures are longitudinal, and separate the lateral parts of the region from the central. The remaining suture joins the centre of the two longitudinal sutures like the cross line of the letter H, dividing the centre of the cephalo-thorax into an anterior and a posterior portion, of which the anterior is the greater. There is also an apparent suture near the frontal margin. The frontal margin is indented, the greatest depth being in the middle line. This indentation to some extent is due to the scar caused by the breaking away of the filament for attachment in the "chalimus" stage. In the centre of the hollow, situated on the ventral surface, is an oval-shaped opening (*b*) with a chitinous fringe. This is evidently a sucker, and represents the remains of a median sucker which is considerably developed during the "chali-

mus" stage, when the maxillipedes are rudimentary. Probably in the adult it acts as a first aid in securing the animal to its host. Passing backwards from this sucker, but distinctly over it, there is a transparent rod (*c*, fig. 1, Plate I.; fig. 3, Plate III.), lying inside a triangular blood space, which terminates in a gland (*c g*, fig. 3, Plate III.). The gland is probably the organ that secretes the substance for the filament in the "chalimus" stage and the rod the remains of the filament. The filament and duct are in actual contact during the early part of the parasite's life (Plate I., figs 4 to 6, *c*). The eyes, two in number, are situated in the middle of the cephalo-thorax. The frontal and lateral margins are surrounded by a transparent membrane with faint transverse lines. This membrane is simply an extension of the chitinous exoskeleton which covers the whole animal. It has frequently a serrated edge caused by tearing.

The second part of the body is very small, and represents the fourth thoracic segment of the pelagic Copepoda. The fourth feet are attached to the external margins of this segment.

The third part of the body known as the "genital segment," is of variable shape, according to the degree of maturity of the reproductive organs. In an immature female (Plate II., fig. 6), it is usually very little larger than the fourth part, whilst in a mature one it is nearly as large as the cephalo-thorax. The genital segment of a mature female is somewhat quadrangular in outline, slightly wider posteriorly than in front. The same segment in a mature male (Plate I., fig. 2) is oval in shape and about one-third wider than the fourth part.

The fourth part of the body is short and narrow, being only one-fourth of the width of the female genital segment, and corresponds to the abdomen of the pelagic Cope-

poda. There is an incomplete articulation near the middle. At the apex of the abdomen there are two short papillæ known as the furca or caudal stylets, which usually have four or five plumose hairs on their posterior margins.

There are twelve pairs of appendages* (Plate II., fig. 1) as follows:—One pair of antennules, one pair of antennæ, one pair of mandibles, two pairs of maxillæ, two pairs of maxillipedes, and five pairs of feet, the first three pairs of feet only being adapted for swimming.

The eyes appear as a reddish spot in the living animal, and are situated on the dorsal surface mid-way between the frontal margin and the transverse line of the cephalothorax. When this spot is examined microscopically (Plate III., fig. 13) it is found to consist of two lateral eyes closely approximated, embedded in a mass of reddish-black pigment, and wholly under the carapace. Each eye has a simple, spherical, crystalline lens, beneath a thin cornea. Behind the lens is a row of retinal cells of fairly large size, lined internally with a tapetum or pigment layer. A chitin division lined with deep red pigment separates the two eyes. The earlier Zoologists had considerable doubt as to the true position of the eyes, some even believed the animals were blind. Others mistook the semi-circular suckers on the frontal margin of *Caligus* already referred to for the organs of vision, giving them the name "Binoculus."

The antennules are placed at the external margin, just behind the suture on the frontal plate, and each consists of two joints. The basal joint is much larger than the apical, and is clothed on its upper margin with plumose setæ.

* The minute details of the jointing and setæ of the appendages are not shown in these figures.

The other appendages are all on the ventral surface. The first are the antennæ. These consist each of two joints, a short stout basal one, and an apical one in the form of a strong prehensile claw. The antennæ are used to assist the second maxillipedes in grasping.* The apex of the claw projects into a small cup in front of the first maxillæ.

The mandibles are enclosed in the suctorial mouth (Plate II., fig. 8). They are stylet shaped, and composed of four joints. The apical joint of each mandible is flattened, curved inwardly, and serrated on its inner margin. There is no mandibular palp.

The appendages described here as the first maxillæ are given that name with some doubt. The pelagic Copepoda have only one pair of maxillæ, which correspond to the second pair in this memoir. The identification of the appendages now to be described as maxillæ is based upon the fact that they are innervated by a nerve from the sub-œsophageal ganglion that has its origin just anterior to the nerve supplying the maxillæ proper. The first maxillæ consist of one joint which is considerably swollen at the base, and tapers to a sharp point at the apex, forming as a whole a curved claw. Two minute setæ are attached to the basal part, and probably represent the exopodite or palp. These appendages are situated near the lateral margins, and slightly posterior to the base of the antennæ.

The second maxillæ are placed at the sides of the mouth, and consist of a single joint, robust at the base and dividing into two slightly curved teeth at the apex, representing the exopodite. There is a distinct endopodite, with two setæ at its apex, attached to the base of the anterior surface of the exopodite. The second maxillæ

* Baird (op. cit. p. 263) describes these organs as the first pair of footjaws.

appear to act as a scraping apparatus for removing the skin of the host.

The first maxillipedes consist of two-jointed appendages placed mid-way between the apex of the mouth, when it is at rest, and the lateral margin. Their chief function is apparently to keep the mouth free from obstruction.

The second maxillipedes situated near the middle line, mid-way between the first maxillipedes and the first pair of feet, are composed of two joints. The basal joint is considerably swollen and the apical is in the form of a powerful claw, which closes upon the basal joint, forming a strong grasping apparatus. According to Claus, and others, the first and second maxillipedes are really only the exopodite and endopodite of one and the same appendage.

The first three pairs of feet consist of an endopodite and an exopodite attached to a two-jointed protopodite. In the first pair the endopodite is rudimentary, and is represented by a single minute joint bearing a few setæ at its apex. The exopodite is two-jointed. In the second pair both the endopodite and exopodite are three-jointed. The third pair has the protopodite well developed, forming a lamella. The endopodite and exopodite are very small, the former being composed of two joints and the latter of three joints. Each of the first three pairs of feet is attached to a median sternal plate. The exopodite of the first, and the endopodite and exopodite of the second and third pairs, are provided with a number of plumose setæ along the internal margins of the joints. The dorsal and ventral margins of the protopodites of the second and third pairs of feet are furnished with movable setose plates. The sterna of the second and third feet are clothed with setæ on the posterior margins. The fourth pair of feet (Plate I., fig. 1) have two-jointed protopodites,

and exopodites also two-jointed, but no trace of endopodites. The external angles of the joints are furnished with short spines. The fifth pair are rudimentary, are attached to the posterior end of the genital segment, and consist of a thin lamella, furnished with three setæ along the posterior margin. Situated on the middle line between the second maxillipedes is a strong chitinous plate with a bifid apex pointing posteriorly. This is known as the sternal fork, but its function is unknown.*

The external openings are the mouth, the vulvæ, the openings of the oviducts and vasa deferentia and the anus. The mouth (Plate II., fig. 1 and fig. 8) is situated on the ventral surface of the cephalo-thorax, and is placed at the apex of a short, movable, conical tube. This tube is composed of the upper and lower lips fused together. The vulvæ (Plate II., fig. 6) are situated on each side of the middle line near the posterior end of the genital segment, and communicate with the "receptacula seminis." They are difficult to see in the adult female, but have each frequently a spermatophore attached which indicates the position. The openings of the oviducts are in the same segment, but nearer the lateral margins and just under the fifth feet. The openings of the vasa deferentia (Plate II., fig. 5) are situated on the postero-lateral margins of the genital segment of the male. The anus is situated in the middle line at the apex of the abdomen. In addition to these more important openings, there are also apertures of pore-canals and glands on the anterior surface of the basal joint of the protopodites of the second and third pairs of feet, and also on the dorsal surface of cephalo-thorax and abdomen. The opening in some cases

* Mr. I. C. Thompson suggests that the sternal fork appears to him to be a support or crutch, serving to raise the body sufficiently from the host to enable either the swimming feet or the mouth organs to be used, but I have not seen it used in this manner.

is at the apex of a small papilla, and communicates with a sac in the interior (Plate II., fig. 11).

When resting, *Lepeophtheirus* lies upon the ventral surface, keeping the first three pairs of feet moving with spasmodic jerks. When irritated, as in attempts to remove them from their host, the males and immature females move very rapidly over the skin of the fish. The mature females make no attempt to escape, only clinging more securely. On transferring them to clean sea water they settle on the sides and bottom of the vessel, and sometimes adhere to the surface film of the water, remaining quiescent for long periods. When the water is shaken slightly they detach themselves and swim about rapidly on their backs. They soon tire, however, and return to rest again. *Lepeophtheirus* makes no attempt to leave the water when kept in small aquaria. The allied form, *Caligus*, on the other hand, crawls out of the water and up the sides of the glass, where it remains, making no attempt to return, and soon dies owing to the evaporation of the water from under the carapace. These parasites are very tenacious of life, and live for a considerable time after the host has died if they are not allowed to dry up. In some instances, although the host had been dead over twelve hours, and the parasites to all appearance were also dead, they soon revived when placed in sea water. Increase of temperature to 16° C. and over is fatal to them. They can, however, stand very considerable decrease of temperature. On one or two occasions during February, 1900, the small aquaria in the tank room at Piel, some of which contained parasites under observation, were frozen, and the temperature of the room itself stood at —1° C., but the parasites suffered no harm. They can also be kept alive in sea water for weeks without change if the aquaria are kept cool.

The colour of the living animal varies with the position in which it lives. On the dark side of the fish they are of a deep brown, almost black, colour. On the "white" side and under the fins they are nearly colourless, due to the contraction of the pigment cells, which appear as brown spots under the microscope. The dark coloured forms soon become almost colourless when exposed to light.

The Body-wall and Body-cavity.

The body-wall consists of (1) the chitinous cuticle or exoskeleton, which has been described in the external characters, (2) the cellular hypodermis, and (3) the connective tissue laminæ which line the integument, traverse the body cavity, and support the alimentary canal and other organs. The only cavity left inside the body-wall is the system of lacunæ, in which the colourless blood flows (see below under blood system, p. 20).

The Alimentary Canal.

The mouth, already described, leads into a short, narrow curved œsophagus, lined with a thin chitinous coat which is continuous with the exoskeleton. Near the anterior end the chitinous coat is much folded. The œsophagus (Plate III., figs. 3 and 5) passes through the anterior part of the nervous system, and in a transverse section of that region appears as a minute pinhole. After leaving the nervous system, it courses over the sub-œsophageal ganglion, and under a short cæcal projection of the stomach, finally entering the stomach on its ventral aspect, at the posterior end of the sub-œsophageal ganglion.

The stomach lies along the ventral surface, and is lageniform in shape (Plate II., fig. 3). At the anterior end it is produced into a short cæcum which extends over the posterior end of the œsophagus and it terminates by

opening into the intestine in front of the second pair of feet.

The intestine is the direct continuation of the stomach. It commences in front of the second pair of feet, and passes through the thoracic and genital segments into the abdomen. It widens slightly behind its junction with the stomach, and then contracts as it passes through the fourth thoracic segment. It expands again in the genital segment, and contracts as it enters the abdomen. It terminates in a short rectum leading into the anus at the apex of the abdomen. There are no convolutions in this alimentary canal.

The intestine at its anterior end lies on the ventral surface of the animal. In the centre where it passes through the genital segment, it courses along the dorsal surface. It bends down as it approaches the abdomen, and occupies the centre of that part of the body. In transverse sections of a mature female the stomach is triangular in shape, with the apex pointing dorsally. The intestine in the genital segment is also triangular in transverse section, but the apex is directed ventrally. In immature females the stomach and intestine are of almost circular outline when cut transversely, so that the alimentary canal is considerably compressed when the reproductive organs arrive at maturity.

The wall of the whole alimentary canal is lined with a thin layer of chitin continuous with the exterior. In many places it is considerably broken up, giving it the appearance of fine striation. Underneath the chitin is a layer of nucleated cells, which extends from the posterior portion of the œsophagus to the rectum. There does not appear to be any marked regional differentiation in the cells. The lining of the stomach and intestine is thrown into a number of longitudinal folds (Plate III.,fig. 11), the

height of which varies considerably. In the anterior portion of the stomach these folds are very little higher than the general line, but as they pass posteriorly they increase considerably, diminishing again in the intestine as they approach the rectum. The greatest height of the folds is reached in the portion of the intestine passing through the genital segment. In the intestine and posterior portion of the stomach there are a number of glandular cells, usually at the apices of the longitudinal folds, the contents of which stain deeply with eosin. In many of these the cell contents have disappeared, leaving a clear space, only the cell wall remaining.

The wall of the stomach and intestine is marked by a series of transverse constrictions, giving it a crenate appearance, which is easily seen in the living animal. In the living animal an intermittent movement of the intestine and stomach is kept up. The action is wave-like, starting at one end, and passing to the other. After continuing in one direction for a time, it reverses and passes the opposite way. There is no valve between the stomach and intestine, and when the peristaltic motion is reversed the fluid in the intestine is sent back into the stomach again. The only portions of the alimentary canal that can be closed are the œsophagus and anal end of the rectum. The former is controlled by two longitudinal muscles which compress it, the latter by a number of muscles passing obliquely to the body-wall at the sides of the abdomen. The fluids contained in the alimentary canal are usually colourless, but occasionally when taken direct from the fish and placed under the microscope, a reddish tint may be detected at the posterior end of the œsophagus.

In connection with the alimentary canal there is a distinct paired digestive gland (Plate II., fig. 3 and fig. 9).

It consists of three portions, two moderately large masses on the lateral margins of the cephalo-thorax, just behind the antennules, and a median, smaller one, in front of the base of the mouth. The lateral portions are connected with the median by a duct. The median portion gives off a duct. which passes posteriorly along the œsophagus and enters the cæcum at the anterior end of the stomach. When the parasite is first removed from the fish the digestive gland is usually of a dark brown colour, but after starving for a few weeks it becomes colourless. The product of the gland is a pale, yellow fluid, which can be seen as it passes along the duct between the lateral and median portions.

Situated between the first and second pairs of thoracic feet is a pair of glands visible in the living animal as brown spots. A minute duct passes downward and then forward along the stomach. The duct appears to enter the stomach near the posterior end.

The food of this parasite is said to be mucus, and blood has not been detected in the stomach.* This fact gives some cause for the opinion advanced by many Zoologists that *Lepeophtheirus* and other allied genera are therefore not parasites in the strict sense of the term, and may not be hurtful to their hosts. There is considerable difficulty in settling the question of their true food. Specimens taken direct from the living fish and placed under the microscope, rarely show even the faintest trace of red colouring matter in the alimentary canal. The difference in structure between the Caligidæ and the obviously blood-sucking Lerneæ is very great. This will be pointed out in the section dealing with *Lernæa branchialis,* and may account for the apparent absence of blood. Mucus at the best is a poor food, but *Lepeophtheirus* can live for upwards

* They do not hesitate, however, to eat their comrades when these become feeble.

of six weeks in filtered sea water without visible food of any kind.

From the large numbers of flounders examined in the Piel laboratory, partly in connection with this memoir, but chiefly in connection with fisheries work, during the past year or two, the conclusion has been arrived at, that *Lepeophtheirus pectoralis* to some extent feeds on blood, and may be hurtful to the fish, especially when present in numbers (see figure on p. 6).

The appendages are more suited for a sedentary life than even a semi-pelagic one. The animals can only remain swimming for short periods, and their presence in tow-nettings, therefore, is accidental. They do not, under normal conditions, and as long as the fish remains in a healthy state, leave their host. In the fish tanks at Piel over 150 flounders, all more or less infested with *Lepeophtheirus*, are kept during the spawning season. The waste water from the tanks is carefully filtered for periods of at least three months in the spring, to collect the eggs shed by the fish. Yet not even one specimen of the parasite has been found in the filter. When the fish are examined and the parasites removed, no matter how carefully, the skin, especially where there are a number close together, is usually lacerated and bleeding. The males and immature females on the general surface of the body do not seem to remain long enough in one place to cause obvious injuries. Under the fins, however, and on the fins themselves, where the egg-bearing females are usually found, and where they lie for weeks in the same position if not disturbed, is the part of the fish chiefly injured. The pectoral fin in some instances may be partially destroyed, and pieces of the tissues are frequently found enclosed in the second maxillipedes of the parasite.

The antennæ and claws of the second maxillipedes are plunged into the tissues of the fish along with the teeth of the maxilla, lacerating the skin, and into this wound the suctorial mouth is directed. The blade-like mandibles assist in collecting the particles of food material. These are sucked up, pass down the œsophagus into the stomach, where they are at once acted on by the fluid from the digestive glands, and the colour of any blood present may then be discharged. It is usually at the junction of the œsophagus with the stomach that any red coloured particles occur. The food can then be traced along the stomach and intestine, and the waste matter is expelled from the anus in long strings.

On comparing transverse sections of the alimentary canal of *Lepeophtheirus* and of *Lernæa* which happen to contain food, and have been stained in eosin and hæmatoxylin, there is seen to be a marked similarity in the nature of the food in the two cases. Both are finely granular, and stain red with eosin. Mucus from the flounder has no such granular appearance.

It is stated by some Zoologists that copepod parasites are generally found most abundantly on weak and diseased fishes. It is not so with *Lepeophtheirus pectoralis.* Flounders with many parasites in our tanks were in as good condition as those that had none. They were never found on flounders which were thin and in poor condition, as they detach themselves and swim away when the fish becomes feeble. This was proved by actual experiments and observations at the Piel Hatchery.

The Blood and Circulation.

There is no heart in *Lepeophtheirus,* nor are there any proper blood vessels.

The circulation is wholly lacunar, and simply consists of broad, irregular streams passing through the spaces left among the internal organs, and between the connective-tissue bands of the body-wall. These streams have in general certain definite directions, but they are not uniform, continuous currents. The fluid advances by successive jerks, depending upon the movements of the alimentary canal and, in part, of the reproductive system. The blood is a clear fluid, containing numerous colourless corpuscles. The corpuscles vary in size and shape, and can accommodate themselves in diameter to the spaces through which they pass.

Plate II., fig. 2, shows the course of the main blood currents. Starting from behind the eye, there are two currents passing posteriorly, one flowing to each postero-lateral angle of the cephalo-thorax, where it turns and courses forward along the lateral margin of the carapace till it reaches the group of muscles connected with the mandibles. It then divides, one portion continuing along the margin to the base of the antennules, where it splits up into minute currents, all converging to the base of the mouth, while the other branch of this cephalo-thoracic current passes along the muscles of the mandibles and duct of the digestive gland, and meets the currents of the former branch at the base of the mouth.

A second main current courses posteriorly through the cephalo-thorax and the fourth thoracic segment, into the genital segment. It flows there along the reproductive organs in a broad stream, and turns round at the end of the segment. The currents from both sides meet in the middle line, and flow forward under the alimentary canal. In the region of the second maxillipede, this median ventral current breaks up into a complicated series of smaller currents, some of which pass into the two currents

flowing posteriorly, and the others into the currents passing to the base of the mouth.

The main currents are easily seen by placing the living animal on its back, in a drop of sea water on a slide then covering with a thin cover glass and examining with a ¼in. objective.

The blood currents described above do not continue to flow for any length of time in the one direction. At one period they may be flowing as indicated by the arrows in Plate II., fig. 2. Then they suddenly slacken and reverse, and stream for a time in exactly the opposite course. Sometimes the blood corpuscles are seen to simply oscillate backwards and forwards, making no advance, but at other times they pass rapidly along in a definite manner.

There are no independent organs of respiration. It has been suggested by Hartog and others that the blood is probably aerated from the sea water contained in the thin-walled alimentary canal by the method of "anal respiration," which has been described in *Cyclops*, *Caligus*, *Argulus*, *Daphnia*, *Cypris* and other lower Crustacea.

The cuticular exoskeleton over the surface of the body is in most places so thick that the respiratory change of gases may be supposed to take place much more readily through the very thin layer of chitin which lines the rectum. There are dilator muscles attached to the wall close to the anus, and the peristaltic movements of the whole alimentary canal may aid in the production of inhalent and exhalent currents of water. It appears, however, to the present author that further precise observations are required to substantiate this hypothesis.

No organ corresponding to the "shell gland" described in various lower crustacea, and shown by Claus, Hartog and others to be a renal organ, has been found.

THE MUSCULAR SYSTEM.

The muscles moving the appendages and segments of the body can be distinctly seen and traced to their extremities through the transparent exoskeleton (Plate II., fig. 1 and fig. 2).

The frontal portion of the cephalo-thorax is controlled by two short slender muscles, *mlf.*, (Plate II., fig. 2) passing postero-laterally from near the lateral edge of the carapace. They act in depressing the margin so as to produce a close attachment to the host. The posterior region of the cephalo-thorax is supplied with a number of pairs of muscles, some passing forward and others laterally, which contract and expand that part of the body. The lateral margins are controlled by long muscles passing obliquely outwards from the anterior end of the lateral suture. The muscles of the fourth thoracic and genital segments arise near the median line of the posterior portion of the cephalo-thorax, and pass backwards. They produce a lateral motion of the posterior parts of the body, and also a sort of telescoping contraction which draws the genital segment into the cephalo-thorax. The muscles of the abdomen arise near the middle of the genital segment and pass backwards. They produce a telescoping movement of the abdomen.

The various appendages and other organs are also well supplied with muscles. The antennules have each a pair, which elevate and depress the joints. The grasping action of the antennæ is produced by muscles passing obliquely to the lateral margins. The movements of the mouth are controlled by a complicated series of muscles passing anteriorly, posteriorly and laterally, all of which assist in elevating and depressing it when sucking up food. The mandibles are provided with muscles of extra-

ordinary length and power, which pass obliquely backward to the lateral margins of the carapace nearly opposite the first pair of feet. The muscles of the first maxillæ are very short and thin. They pass along the posterior surface of the muscles of the antenna, to the lateral margins. The second maxillæ are controlled by powerful muscles passing to the lateral margins. The muscles of the first maxillipedes pass obliquely forward to the lateral margins. The second maxillipedes are supplied with short and powerful muscles which pass forward under the second maxillæ. The terminal claw is provided with muscles of great strength. The first three pairs of feet are supplied with a complicated series of muscles passing dorsally amongst those controlling the posterior portion of the cephalo-thorax. The fourth pair of feet are apparently little used, and consequently are only supplied with feeble muscles. The alimentary canal is controlled by longitudinal muscles, and also by muscles passing transversely, which produce the wave-like peristaltic motions and crenated appearance. The anus is opened and shut by muscles passing obliquely, which open and shut each side alternately or simultaneously according to the requirements of the animal. The reproductive organs are also controlled by muscles, which give rise to pulsating movements, and assist in expelling the ova and spermatophores.

The Nervous System.

The central nervous system in *Lepeophtheirus* consists of a cerebral or supra-œsophageal ganglion and a large sub-œsophageal ganglion placed on the ventral surface, in the median line, and extending from slightly in front of the second pair of maxillæ to near the articulation of the second pair of maxillipedes with the body. The

ganglia are connected by broad commissures passing on each side of the œsophagus, leaving only a narrow opening for its passage. The sub-œsophageal ganglion projects slightly forward under the supra-œsophageal, giving it the appearance of being separated from it, when viewed from the ventral aspect (Plate III., fig. 2). These are the only ganglia, and they supply the various parts of the body with nerves.

The supra-œsophageal ganglion is about half the size of the sub-œsophageal. It is produced on its dorsal surface into an optic lobe (Plate III., fig. 5), from which arises a distinct pair of optic nerves. Horizontal sections of the optic lobe show that the roots of these nerves cross each other (Plate III., fig. 12). Each optic nerve, therefore, is supplied by fibres from both sides of the brain.

The nerves supplying the antennules arise from near the anterior angles of the ganglion. They pass obliquely forward to the base of the antennules, and there subdivide into a number of branches which pass to the setæ clothing the anterior surface of the basal joint and apex of the second (Plate III., fig. 4). From the manner in which the antennules are supplied by this nerve it is evident that they are important sensory organs (Plate III., fig 4).

The antennæ are supplied by nerves arising from the anterior angles of the ganglion, which pass anteriorly under the nerves of the antennules and enter the base of the antennæ. These are the only appendages supplied from the supra-œsophageal ganglion.

The sub-œsophageal ganglion is heart-shaped, and fully twice the size of the supra-œsophageal. It represents the whole of the thoracic and abdominal ganglia of the higher crustacea, and supplies the remainder of the appendages.

The nerves passing to the mandibles have their origin on the anterior margin near the middle line. They course along the muscles of the œsophagus, and reach the mandibles near the base of the mouth.

The next pair of nerves arise at the anterior angle of the ganglion, course forward, under the nerves of the antennæ and antennules, to the frontal plate which they enter about midway between the lateral margin and middle line. They then turn abruptly and pass out to the lateral margins of the frontal plate, just above the antennules. The margin at this point is destitute of the transparent membrane which surrounds the carapace. The nerves terminate in a shallow cup, evidently a sensory organ.

Three other pairs of nerves arise from the anterior angles of this ventral ganglion. The first passes to the rudimentary first pair of maxillæ, the second, a short nerve, passes to the second pair of maxillæ, and the third to the muscles controlling the lateral margins of the cephalo-thorax.

The nerves supplying the first pair of maxillipedes arise from the anterior portion of the lateral margin. They are large nerves at their origin, but immediately divide into four branches, passing to the maxillipedes and muscles. The second pair of maxillipedes are also supplied by nerves arising from the lateral margins. Like those of the first maxillipedes they have strong roots, and at once divide into three branches which pass to the second maxillipedes and their muscles.

The remaining nerves have their roots in the posterior end of the ganglion. There are three pairs. These supply the five pairs of feet and the abdomen. The outer pair of nerves supply the first pair of feet. Near the origin a branch is given off which passes to the muscles

of the stomach. The next pair supply the second pair of feet. They course along the median nerves as far as the sternal fork and then diverge. Just under the sternal fork a branch is given off which appears to pass to the muscles of the posterior region of the cephalo-thorax.

The median pair course close together, and unless carefully examined are easily mistaken for a single nerve. There is a distinct division, however, which is apparent even in the roots. Between the second and third pairs of feet a strong branch is given off which passes to the third pair of feet. The nerves then diverge, and just before entering the fourth thoracic segment give off a branch that passes to the fourth feet. The main trunks course on through the genital segment, still further diverging. Shortly after entering the broad part of this segment a third branch is given off which takes a semi-oval course along the ventral surface of each half of the segment, finally passing to the setæ of the fifth feet. On entering the abdomen the main trunks split into two branches, one passing to the anus and the other to the setæ on the apex of the caudal stylets (Plate III., fig. 2).

Each nerve, after leaving the main trunk, sends out numerous branches which pass to the various muscles controlling the appendages innervated by that nerve. Excepting the nerve passing to the fifth feet, the branches are not shown in the figure (Plate III., fig. 1). There is considerable difficulty in tracing the endings of the branches when they pass amongst the muscles.

The chief sense organs connected with the nervous system are the conspicuous eyes which are described above (p. 71). There are also the numerous setæ scattered over the surface of the body and appendages, which are possibly tactile in function. Probably the setæ upon the antennules, which are richly supplied with nerves from the

supra-œsophageal ganglion, have a special function, which may be olfactory.

The Reproductive Organs.

The reproductive organs are paired, and as already stated, the sexes are separate.

In the female (Plate II., fig. 4) the ovaries are large kidney-shaped organs lying on each side of the anterior portion of the stomach and extending from under the first pair of feet to the base of the second maxillæ, when fully matured. Each oviduct (*od.*) arises near the anterior end of the ventral surface of the ovary, and courses posteriorly as a narrow tube till it enters the genital segment. It then expands rapidly, and passes to near the end of the segment. It then reverses its course, passing forward to the central portion of the segment, where it turns again in a posterior direction, and passing out to the centre of each half of the segment, it opens to the exterior just under the fifth feet. Each oviduct thus forms two loops in the genital segment. On the ventral aspect of the loops of each oviduct there is a short, semi-transparent cylindrical tube (*sg.*) with the anterior end closed and rounded, and the posterior produced into a fine duct, which communicates with the oviduct near its extremity. This organ is evidently a cement gland for secreting the enclosing membrane of the ovisac. Each vulva (fig. 6, *vu.*) is situated near the middle line behind the junction of the genital segment with the abdomen. It appears to consist of a simple opening leading into the vagina which expands into a "receptaculum seminis." This is an elongated sac passing from the median line to the oviduct, which it enters alongside the duct of the cement gland.

In the male the reproductive organs (Plate II., fig. 5) consist of a pyriform testis, on each side, situated in a position corresponding with that of the ovary. It is only

about one-fourth the size of the ovary. Each vas deferens courses posteriorly into the oval genital segment. It communicates with the sac of the spermatophore on the external margin near the posterior end. A short cement gland furnishes a duct which passes in at the anterior end of the sac. The spermatophore, an oval body containing the spermatozoa, is expelled from an opening near the posterior angle of the segment.

In *Lepeophtheirus* the fertilisation of the female is accomplished soon after the "chalimus" stage is completed. The genital segment is then very small, about one-fifth the length of that of a mature female. It is grasped by the male on the dorsal aspect. The antennæ close round the junction of the genital segment with the fourth thoracic, and the second maxillipedes seize the segment immediately in front of its junction with the abdomen. The animals remain in this condition for some time, and can only be separated with difficulty. The spermatophores are discharged in pairs. When they are ready for discharging the male folds the whole of the posterior portion of its body along the ventral surface of the female. The openings of the spermatophore sacs are thus brought in contact with the vulvæ. The spermatophores are then discharged, and being in a viscid condition, at once stick to the female. One end of the covering, probably the last part that leaves the opening, is drawn out into a fine thread, which helps to secure the spermatophore. The spermatophores are not, apparently, always fortunate in reaching the vulvæ. It is by no means uncommon to find them planted amongst the appendages in little clusters like grapes. These have been mistaken by some of the earlier Zoologists for the eggs, when the true egg sacs were considered to be antennules.

One copulation apparently fertilises all the eggs produced by the female. It is obvious, when one compares the male with a mature female (Plate I., figs. 1 and 2), that fertilisation cannot be accomplished when the female genital segment is fully developed. Hence the need of it being effected at an early stage.

The exact period at which the eggs are fertilised by the spermatozoa is unknown. The spermatophores may be found attached to the body for some time after the female has begun to produce eggs (Plate II., fig. 4, *sp.*), but they are then simply empty sacs. Plate II., fig. 7, shows a pair of spermatophores that have been detached from an egg-bearing female. The little opening at *d.* was in direct communication with the vulva. These sacs were empty. In an immature female (Plate II., fig. 6), the vulva leads into a short vagina, passing directly into the oviduct. The spermatozoa probably remain in the vagina which becomes a "receptaculum seminis." In transverse or longitudinal sections through the region of the vagina of a mature female masses of spermatozoa are frequently found in the swollen part (Plate II., fig. 4, *rep.*). The oviduct in the immature female has no communication with the exterior except through the vulva.

The ovary of a mature female appears as shown in Plate II., fig. 10. It consists of a number of tubules lined with nucleated cells representing a germinal epithelium, which will form the eggs. The interior of the tubules is filled with a granular substance, staining faintly blue with hæmatoxylin and eosin. When the eggs become mature the walls of the tubule break down and the eggs pass out into the oviduct. They are then very small, about ·02 mm. in diameter, and do not fill up the duct. They are simply nucleated cells. As they pass posteriorly they increase in size. In the fourth thoracic segment they

measure ·06 mm., and appear as oval bodies with a thin vitelline membrane. The cell contents are finely granular. The nucleus is a large oval body, with a sharp outline. A single rounded nucleolus is also present. After passing into the genital segment the cell contents increase in amount, causing a great enlargement of the egg, which finally passes out at the opening between the vulva and the lateral margin of the segment, already described. As the eggs pass out they are probably fertilised by the spermatozoa from the "receptaculum seminis." They are then enclosed in a thin chitinous tube, secreted by the cement gland, which gradually extends as more eggs are expelled. The ovisacs are often longer than the animal. The eggs in this tube are biscuit-shaped, measuring ·36 mm. in diameter and ·11 mm. in thickness. They are arranged in a single column. When the animal is irritated the tubes are frequently detached. When the embryos hatch, the empty, ruptured tube is left, and remains attached to the animal for a time. After examining many specimens, the conclusion has been come to that additional eggs are not developed in the tubules of the ovary after the first lot have been expelled. Adult females in which the ovary is only an empty sac are not uncommon.

Life History.

Lepeophtheirus has no regular breeding season. Mature females with ovisacs may be found at all times. The state of development reached by the embryos carried by various females collected at the same time is frequently widely different. In some the germinal disc has just begun to segment, in others the larvæ are ready to hatch.

The changes that take place in the developing embryo have not been worked out by the author. The period of

incubation was found to extend over several weeks at least. In one case the ovisacs were kept for six weeks, and in another eight weeks, before the embryos hatched. The incubation takes longer than that, however. In both cases the embryos were pigmented when placed under observation. The first appendages that make their appearance are the antennules, antennæ and mandibles. They are in a rudimentary state, and the embryo is now ready to hatch. During this period the embryo increases in size as it develops.

The whole of the embryos contained in the tube hatch practically at once. The enclosing membrane ruptures, then the membrane of the tube splits, and the nauplii after freeing themselves from the fragments swim to the surface. Plate I., fig. 3, represents a newly hatched nauplius, the natural size of which is ·46 mm. It leads a pelagic life for a time, and grows by successive moultings. It next settles down on some fish, and passes into a cyclopoid state (Plate I., fig. 5). The young parasite immediately develops a thin chitinous filament from the median frontal gland already described, which passes into the tissues of the host, and it becomes fixed. The median sucker (*b.*, Plate I., fig. 5), with the help of the rudimentary antennæ and second maxillipedes, enables the animal to bring its mouth into contact with the host.

If young plaice, flounder, cod, &c., one to three inches in length, be examined very carefully at the end of the summer, it is practically certain that some recently attached *Lepeophtheirus* or *Caligus* will be found either on the fins or some other part of the integument. On examining fins which have parasites attached, the filament is seen passing through the skin, under it, and along one of the fin rays, as shown on Plate I., fig. 5 (natural size ·77 mm.). The filament may have the end bluntly

pointed or flattened into a disc (Plate I., fig. 4). This is the "chalimus" stage referred to on previous pages, so called because Burmeister, in 1831,* described it as a new genus under the name "Chalimus." This was afterwards shown by Hesse and others to be only a young stage of the Caligidæ. The young parasite continues to grow by successive moultings, and the various appendages make their appearance in regular order. The duration of this attached stage has not been determined. When the appendages are fully developed, as in Plate I., fig. 6, the filament separates at its junction with the frontal margin leaving a notch, the remains of which persist all through the adult life.

The male, at the conclusion of the attached stage, is practically fully developed. The female remains in an immature condition until fertilisation is effected and the ova begin to pass down the oviducts. The genital segment then increases in size from that shown on Plate II., fig. 6, to the mature condition of Plate I., fig. 1.

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* Nov. Act. Acad. Natur. Cur. Bonn., vol. xvii., p. 294.

II.—LERNÆA.

The LERNÆIDÆ, although not so extensive a family in numbers of genera and species as the CALIGIDÆ, are more interesting to the specialist. They present some of the most remarkable instances of retrograde development that are to be found in the whole group of parasitic Copepoda. There is great excuse for the difficulty experienced by the earlier Zoologists in giving certain members of this family their true place in the animal kingdom. The fact that these animals were placed first in one group and then in another by successive workers is not surprising, considering that nothing was then known about their life history. It requires some study even at the present day to show that *Lernæa* is a Crustacean, still more to demonstrate that it is related to *Lepeophtheirus.*

The genus *Lernæa* as it now stands contains only five species. Formerly it was very extensive, and included many forms, such as *Lepeophtheirus pectoralis,* that had not the least apparent resemblance to each other in the adult state. Careful research, along with a better knowledge of the minute structure, gradually eliminated the unlike species, which were removed to other genera. An excellent historical account of our knowledge of the group will be found in Baird's "Entomostraca."

The species described here is *Lernæa branchialis,* Linn.

MODE OF OCCURRENCE.

The adult female is found on the gills of the Gadidæ, such as cod, haddock and whiting. Immature (cyclops stage) males, and females with adult males attached, are found on the apex of the gill filaments of the flounder, sometimes in large numbers. Full-grown females are not plentiful on the fishes caught in the vicinity of Piel.

Two to four specimens have been found after examining numerous catches of young cod of one dozen each. The ratio thus varies from one in three fish to one in six. In one or two instances two and sometimes three specimens were found on young cod eight inches long. The length of a full grown female *Lernæa* is a little over one inch.

The adult female is securely fastened to its host by strong branched horns, three in number, which are buried in the tissues of various parts of the gill arches. In many instances the head was found to have actually penetrated the ventral aorta. To obtain the specimens in an entire condition the tissues of the host have to be carefully dissected. Attempts to remove them by force always result in the head being left in the fish. The parasite, when once fixed, remains in the same position throughout life. When it dies the softer parts decay, but the head continues for a long time embedded in the tissues of the host, and is often met with there when dissecting out living specimens.

External Characters.

The adult female (Plate IV., fig. 1) is cylindrical. It is unsegmented, but roughly divided into three parts—a globular head with anchor-like processes, connected by a narrow neck to a much swollen posterior part.

The globular head corresponds to part of the cephalo-thorax in *Lepeophtheirus*. It is furnished with three more or less branched horns, two lateral and one median and dorsal. The head is slightly curved downwards, terminating in a conical apex.

The anterior portion of the neck represents the remainder of the cephalo-thorax and the fourth thoracic segment. The whole of the neck is marked by fine transverse lines.

The remainder of the neck and the greater part of the swollen mass behind corresponds to the genital segment. The abdomen is represented by the terminal portion of the swollen part, and gradually tapers to a blunt end. The swollen region of the genital segment is abruptly bent into the form of the letter S (Plate IV., fig. 1).

The appendages are rudimentary, the greater number being entirely absent. Those present are the first pair of maxillipedes placed at the apex of the head, immediately under the mouth, and four pairs of swimming feet at the anterior end of the narrow neck. The swimming feet are exactly as they exist in the cyclops stage both in size and structure. The protopodite is two-jointed, the exopodite of the four pairs is two-jointed. The endopodite of the first two pairs is also two-jointed. The third and fourth pairs of feet have no endopodite.

The external openings are, the mouth placed at the apex of the head, the openings of the oviducts situated on the ventral aspect of the S-shaped region, and the anus at the blunt apex of the abdomen (Plate IV., fig. 1, *an.*).

The colour of the living animal is dark red, due to the contained blood. When removed from the fish and placed in sea water the colour changes to white. *Lernæa* does not live long after being taken from the fish. The longest period observed was about twelve hours. They are simply inert sacs quite incapable of movement. Occasionally the parasites are covered with colonies of hydroids which sometimes entirely obscure them. The exoskeleton consists of a chitinous cuticle moderately thin and soft in the region of the swollen part, but thick and hard on the neck and head.

Immature *Lernæa branchialis* living on the apex of the gill filaments of the flounder (Plate IV., figs. 3, 4, and 5) are cyclopoid in appearance. The animal is oval in trans-

verse section. It is composed of five distinct parts—an oval cephalo-thorax, three thoracic, and one terminal segment, representing the genital segment and abdomen. The anterior portion of the genital segment in the female is indistinctly divided into eleven joints.

The cephalo-thorax attains its greatest width just behind the eyes; beyond that point the sides converge until they reach the first thoracic segment. The cephalo-thorax is produced anteriorly into a broad blunt rostrum. In the very early cyclops stage (Plate IV., fig. 3), the rostrum is further produced into a short triangular filament which secures the parasite to its host. The eyes (Plate V., fig. 3) are situated on the dorsal surface a short distance behind the rostrum. In the living animal they appear as a dark red spot with a crystalline lens projecting slightly at each side. When examined microscopically the structure is found to be the same as that described in *Lepeophtheirus*. A thin cornea encloses a spherical crystalline lens. Behind the lens a row of fairly large retinal cells is lined internally with a tapetum layer. A chitinous septum lined with deep red pigment separates the two eyes. The appendages attached to the cephalo-thorax are as follows:—

The antennules are placed at the posterior angles of the lateral margins of the rostrum. They are short, and are composed of four nearly equal joints furnished with fine setæ.

The antennæ are composed of two joints. The apical joint is provided with a strong claw on its external angle. The antennæ usually project beyond the rostrum, and it is by means of these that the attachment to the host is maintained when the filament is broken off.

The mandibles are not enclosed in the suctorial mouth. They are situated at the base of the lateral surfaces of the

conical tube of the mouth, and consist of two parts. The basal joint is cylindrical. The second joint is flattened, and terminates in a broad blade, which is serrated on the inner margin.

The single pair of maxillæ are placed at the base of the mandibles. They consist of two lobes, one of which is very small. The larger lobe has two moderately long setæ at its apex, the smaller one has one seta.

The first pair of maxillipedes are placed immediately behind the mouth. They consist of four joints, the last joint being furnished with a strong claw. The basal joint has two short hooks near its apex.

The second pair of maxillipedes in the female are rudimentary, and are represented by a minute knob. In the male they are composed of two joints, the apical one being in the form of a powerful claw. It is by the aid of the second maxillipedes that the male grasps the female during copulation.

The first pair of swimming feet consist of a two-jointed protopodite, an endopodite and an exopodite, both two-jointed. The apical joints of the endopodite and the exopodite are furnished with long plumose setæ on their inner margin and apex. This pair of feet is attached to the posterior end of the cephalo-thorax.

The second pair of swimming feet is attached to the first free thoracic segment, the third pair to the second free thoracic, and the fourth pair to the third. These free segments really represent the second, third and fourth thoracic segments, the first being a part of the cephalo-thorax. The second pair of swimming feet in every respect resemble the first pair. The protopodites of the third and fourth pairs are two-jointed; the endopodites in both pairs are absent. The exopodites are similar to those of the first and second pairs. The fifth

pair of feet is represented by minute papillæ. The caudal stylets are very short, and furnished with three or four short plumose setæ at the apex.

The external openings are the mouth, the vulvæ, the openings of the vasa deferentia and the anus.

The mouth is situated on the ventral surface of the cephalo-thorax, at the apex of a conical tube, composed of the upper and lower lips fused together. In the very early cyclops stage the lips are not fused. The vulvæ and openings of the vasa deferentia are placed at the posterior angles of the genital segment. The anus is at the apex of the abdomen, in the middle line. The vulvæ open into the receptacula seminis, which are in direct communication with the oviducts.

The whole of the genital segment and abdomen in the female is marked by fine transverse lines. The colour, which is arranged in patches, varies from dark violet to light red.

Alimentary Canal.

In the adult the mouth opens into the intestine, which probably acts as the stomach, the œsophagus and true stomach having disappeared in the metamorphosis of the cephalo-thorax. The intestine is at first narrow where it passes through the neck, then it widens considerably in the swollen part of the genital segment, contracting slightly in the abdomen, and finally terminates in a short, narrow rectum leading to the anus (Plate V., fig. 4). The intestine is lined with a single layer of nucleated cells. Attached to this layer, and in some cases embedded in it at irregular intervals, are large cells filled with fine granular material. In some parts these large cells are grouped together two and three rows high. In other parts they are quite free (Plate V., figs. 5 and 6). The layer supporting the nucleated cells appears to be com-

posed of fine muscle fibres. There is no chitinous inner lining as in *Lepeophtheirus*. Between the basement layer of the intestinal wall and the integument there is a network of muscles passing in various directions. This tissue represents the body-cavity and body-wall. The spaces between the muscles are filled with the red blood. The peristaltic movement of the intestine is similar to that observed in *Lepeophtheirus*.

In the cyclops stage the mouth leads into a short, narrow œsophagus (*œ*, Plate V., fig. 2), which passes into the comparatively wide stomach on its ventral aspect. The stomach is lageniform, with the narrow end pointing posteriorly. On the dorsal aspect, at the anterior end, it is produced into a short, blunt cæcum. The narrow end of the stomach connects with the intestine, a long straight narrow tube, greatly compressed over the region of the receptaculum seminis. The intestine terminates in a very short rectum leading to the anus. The cells both free and attached along the wall of the stomach and intestine are similar to those in the adult. Sometimes the stomach is filled with free cells, which are kept constantly travelling backward and forward by the movement of the intestine. At other times few free cells can be seen. No trace of blood between the alimentary canal and the integument, as found in the adult, has been observed in the young.

No trace of a digestive gland could be found in the adult. In the young it is probably represented by a series of groups of cells running along the lateral margins of the cephalo-thorax (Plate V., figs. 1 and 3, *l.v.*). A short duct could be traced leading from these groups into the stomach, just posterior to its junction with the œsophagus.

When the alimentary canal of a living parasite is opened, and the free cells are isolated and examined with

a high power, they are found to be subspherical, granular, and of various shades of greenish yellow colour. Some of the cells exhibit faint amœboid movement. It is probable, therefore, that the digestion is intracellular.

The food of these parasites is undoubtedly blood which we find in the alimentary canal, but whether the absence of digestive glands in the adult accounts for its unchanged appearance has not been ascertained. In the young, where there is an apparent digestive gland, the contents of the alimentary canal are not red.

Circulation and Respiration.

There is no heart or vascular system, and in the adult no movement of fluids could be observed which would indicate a blood circulation. The animal is probably dependent upon the blood sucked from its host for the supply of oxygen necessary to maintain life. It is therefore possible that the early death after removal from the fish is due largely to the inability to take up oxygen from the water. The blood circulation could not be satisfactorily traced in the cyclops stage.

The Muscular System.

The muscular system in the cyclops stage, although not so highly developed, is practically similar to that of *Lepeophtheirus*. In the adult female it is simply a network between the integument and the alimentary canal forming a supporting medium for the latter.

The Nervous System.

In the cyclops stage the central nervous system is the same as in the adult *Lepeophtheirus*. The nerves supplying the various appendages have also the same origin and direction as described in that type. The nerves marked 4a, 4b, and 5a in Plate III., fig. 2, could not be traced.

The nerve supplying the antennules has a similar branching at its termination to that of *Lepeophtheirus.*

In the adult *Lernæa* no trace of a nervous system could be made out, and certainly if present at all it is very much reduced.

THE REPRODUCTIVE ORGANS.

The reproductive organs of *Lernæa,* like those of *Lepeophtheirus,* are bilaterally symmetrical. In the cyclops stage of the female (Plate V., fig. 1) the ovaries (*o.*) are pyriform organs lying on each side of the stomach. They are situated on the ventral surface near the posterior end of the cephalo-thorax. Each oviduct (*od.*) arises near the posterior end, and courses posteriorly as a narrow tube. When it enters the genital segment it expands rapidly, ending in a large sac, the receptaculum seminis (*s*), communicating with the vulva (*vu.*). The oviduct has no distinct loops, and no cement gland is found.

In the adult male (Plate IV., fig. 5) the testes (*t.*) occupy the same positions as the ovaries in the female. The vasa deferentia are straight, narrow tubes coursing posteriorly and terminating in the sacs of the spermatophores. A cement gland is present, as in *Lepeophtheirus.*

The ovary in the course of the metamorphosis undergoes great change of position. It is removed from the cephalo-thorax into the genital segment. It occupies a narrow region at the apex of the deep indentation (Plate V., figs. 4 and 5, *o.*). The two ovaries have also practically fused together, no separation is visible in transverse section. The united ovaries are produced into horn-like projections anteriorly and posteriorly (Plate V., fig. 5). The oviducts (*od.*) arise near the apex of the anterior horns, pass across the segment to its ventral surface, and then

course along each side of the median line to the external openings. Each cement gland (Plate V., figs. 4, 5 and 7, *sg.*) is a long crystalline organ of nearly the same length and breadth as the oviduct, lying ventrally to it. The anterior part terminates at the base of the neck, in a blunt end. The posterior end communicates with the oviduct just inside the opening to the exterior.

The structure of the ovary of *Lernæa* differs considerably from that of *Lepeophtheirus.* In the cyclops stage it consists of a mass of minute nucleated cells. In the adult condition there are no tubules, and all the eggs are in close contact. The size of the eggs in the ovary of the adult varies from ·04 to ·08 mm. They are of the same structure and undergo the same changes in their passage along the oviduct as the eggs of *Lepeophtheirus* when they enter the thoracic ends of the oviducts. The ovisacs consist of long slender tubes very much twisted. (Plate IV., fig. 1, *os.*). When straightened out each tube is often found to attain the length of seven or eight inches. The eggs are arranged in a single column, and the period of incubation is of the same duration as in *Lepeophtheirus.* The death of the parent or detachment of the ovisacs has no effect on the vitality of the embryos.

Fertilisation of the female is effected during the fixed period of the cyclops stage. The spermatophores are attached to the female in a similar manner to that described for *Lepeophtheirus.* The contents pass into the receptacula seminis, and the empty sacs fall away. They are then replaced by others in succession, until the receptacula are filled. Each fully charged receptaculum represents the contents of four spermatophores (*rep.*, Plate IV., fig. 4). At first there is a distinct division between each lot, but this soon disappears, and the whole becomes one mass of spermatozoa. From a large number of

females sectioned in various directions, the conclusion has been arrived at that the spermatozoa at once pass up the rudimentary oviduct to the ovary and fertilise the eggs. This probably accounts for the difference between the ovary of an adult *Lernæa* and *Lepeophtheirus*. No trace of a receptaculum seminis could be made out in the adult.

Life History.

The development of the embryo has not been worked out by the present author. An excellent work by D. Pedaschenko* contains a full description and figures of the developing embryo.

The young *Lernæa* hatches out as a nauplius, with three pairs of appendages, representing the rudimentary antennules, antennæ, and mandibles (Plate IV., fig. 2, nat. size, ·45 mm.). It then after a short pelagic life, settles on the apex of the gill filaments of the flounder, to which it adheres by a broad chitinous filament, and passes into a cyclopoid form (Plate IV., fig. 4). The young *Lernæa* are occasionally found on the gills of the plaice and lumpsucker. The parasite, by its attachment to the gill filament, produces a marked change in that organ. The whole of the apex assumes a tumid character, and the filamentous plates on both sides for some little distance disappear (Plate IV., figs. 8 and 9). While attached to the gills the various appendages develop. The male here reaches maturity (Plate IV., fig. 5), and undergoes no further change. In the female a considerable lengthening of the genital segment accompanies the appearance of the various appendages. Fertilisation next takes place; then the young female severs its connection

* Development of the embryo and metamorphoses of *Lernæa branchialis*. Trav. Soc. Imp. des Naturalistes de St. Petersbourg, vol. xxvi., livr. 4, No. 7, Sect. de Zool. et de Physiologie, 1898. (In Russian, with German resumé).

with the chitinous filament, and leads a pelagic life (Plate IV., fig. 4. Nat. size 2·3 mm.). This condition is frequently found in collections of plankton, and unless care be taken may readily be confused with immature stages of allied forms. I. C. Thompson, F.L.S.,† was the first to recognise certain copepods taken in collections of plankton from Liverpool Bay, &c., as the young of *Lernæa*, from Claus' figures. The presence of the males of *Lernæa* in plankton is to some extent accidental, as only the females lead a pelagic life. The males remain on the gills after the females have gone. The result of the examination of the contents of a fine filter, through which the waste water was passed from the tanks containing flounders in the Piel Hatchery, showed that females were always more numerous than males. The ratio, after a number of trials, was found to be one male to twenty-five females.

At the conclusion of the pelagic life the young *Lernæa* again fixes itself to the gills of a fish, and the retrogressive metamorphosis commences. The parasite buries its cephalo-thorax into the tissues. This region then develops into horns, which are situated one at each side and one dorsal. These pass out at right angles to the body into the tissues of the host. At first they are simple, but by gradual division in each horn they acquire the characters found in the adult (Plate V., fig. 8). The anterior part of the segment curves over, taking up the position shown on Plate V., fig. 4. The eyes, antennules, antennæ, mandibles and maxillæ disappear, leaving only the first maxillipedes, which are represented by small hooks in the adult. The free thoracic segments fuse, but the feet remain as in the cyclops stage. The genital segment elongates until fully fifteen times the original

† Revised Report on L.M.B.C. Copepoda. Trans. L'pool Biol. Soc., vol. vii., p. 212.

length. The abdomen only lengthens a very little. The elongation takes place during the development of the horns and before the eyes and the other organs disappear. This condition is shown on Plate IV., fig. 6; the nat. size is 11·4 mm. The next phase, represented on Plate IV., fig. 7. shows that the development of the horns, the disappearance of various appendages, and the great lengthening of the genital segment is followed by a looping of the posterior region of the latter. This loop gradually expands, and finally takes on the adult condition.

In the metamorphosis of the cephalo-thorax the ovaries are thrust into the genital segment, and take up a position on the dorsal aspect of the posterior region of that segment, in such a manner that the more anteriorly placed portion of the ovary in the adult is what was the posterior part in the cyclops stage (see Plate V., figs. 1 and 4).

The cyclops stage of *Lernœa* was first found *in situ* by Metzger,* who published a short note on the observations made and the conclusions arrived at early in 1868. Claus† later on in the same year, from specimens supplied by Metzger and fresh material, confirmed the observations of that Zoologist.

Concluding Remarks.

In the account set forth on the above pages, it will be seen that there are remarkable differences between the changes that take place in the life history of the two copepods before they reach maturity. In the one case (*Lepeophtheirus*) the life history exhibits a series of progressive developments. In the other (*Lernœa*), although

* Ueber das Männchen u. Weibchen der Gattung *Lernœa*, vor dem Eintritt der sog. rückschreitenden Metamorphose. Jany., 1868.

† Beobachtungen ueber *Lernœocera*, *Peniculus*, und *Lernœa*. 1868.

for a time it advances, yet after a particular period has arrived the remainder of its development is retrogressive. The various appendages in each parasite are developed in the same order. In the one they become perfected when the creature is fully developed. In the other, long before the animal has reached maturity some have disappeared, the remainder continue in a rudimentary condition, and it is incapable of further movement. The internal organs of both copepods are developed in the same way. In one they continue advancing until perfected, and the animal is thus capable of living for considerable periods apart from its host. In the other, such organs as the digestive gland, the brain and nerves, and the blood system become rudimentary, if they do not altogether disappear. The ovary loses its original position and passes into the genital segment. The animal dies when removed from its host.

If only the adults were known, it would practically be impossible to recognise that such a form as *Lernæa* was in any way related to such a typical free-swimming Copepod as *Calanus*, and it would therefore still occupy an uncertain position. But when the whole life history of both copepods is known, tracing the connection becomes comparatively easy. Both originate from a free larval stage known as the nauplius, which has been regarded as the representative of a far back common ancestor. Both pass through a cyclops stage. The one ancestral cyclops form, we may suppose, by maintaining a free swimming life, gradually acquired more perfect appendages, and became at last the form now known as *Calanus*. The other cyclops form by adopting a sedentary life, and depending on other animals for its food, became semi-parasitic like many of the ascidian- and sponge-frequenting forms of copepoda. The transition from *Lichomolgus*-like copepods to such forms as *Bomolöchus*

and *Ergasilus* became simple. Further change in form and habit continued as the various appendages, through constant rest, degenerated. The animal became in consequence more and more dependent on its host for food. Such changes extending over a long period of time, have apparently resulted in such a form as *Lernœa*.

Some Zoologists divide the fish parasites into blood-suckers and mucus-eaters, on account of the apparent presence or absence of blood in the alimentary canal. It is doubtful if such a division is really satisfactory. The probability is that they are all blood-suckers in different degree, and that the presence of blood is only obvious because certain organs are absent. *Lœmargus muricatus*, one of the *Caligidœ*, appears to make excavations into the skin of its host, *Orthagoriscus mola* (the short sun-fish). Several individuals are usually found in each excavation.* No obvious appearance of blood can be observed even in these parasites.

One or two parasites on a fish may not be hurtful, but when the numbers increase they probably have an irritating effect, and finally, when they remain in one position for some time, the skin and tissues become lacerated. Consequently even such external parasites as have been regarded as harmless mucus-eaters may really have an injurious effect upon the fish.

There is much opportunity for investigating the internal structures of the various families of fish parasites. The most of the literature hitherto published deals with the external characters only.

The specimens necessary for the work connected with this memoir have been almost entirely collected from fish caught in the vicinity of Piel. The author is indebted to Mr. R. Newsham, Jun., the Laboratory Assistant at Piel,

* A. Scott. Trans. Nat. Hist. Soc., Glasgow, vol. iii., part 3, p. 266. 1892.

for help in collecting. The important stage of *Lernæa*, shown on Plate IV., fig. 6, is drawn from a specimen sent by Mr. T. Scott, F.L.S., the author's father. It was found on the gills of a whiting caught in the Bay of Nigg, Aberdeen, in 1900, and was the only one met with in the course of these investigations.

Explanation of Plates.

Reference Letters.

a. antennule.
a$^{i.}$ antenna.
a$^{ii.}$ lateral frontal sucker.
an. anus.
b. median frontal sucker.
bls. blood space.
c. filament duct.
cg. filament gland.
cn. chitin.
D. dorsal.
d. opening of spermatophore.
e. eyes.
f. filament.
g. ganglia.
gl. gland
i. intestine.
K^1 left anchor process.
K^2 median ,,
K^3 right ,,
L. left.
ld. duct of digestive gland.
lns. lens.
lv. digestive gland.
M. mouth.
m. mandible.
ml. muscle.
ml.a. antennule muscles.
ml.an. anal muscles.
ml.f. frontal muscles.
ml.i. intestine muscles.
ml.l. lateral muscles.
ml.m. mandible muscles.
ml.mxp. first maxillipede muscles.
ml.pt. posterior cephalic muscles.
ml.rt. rectum muscles.
ml.st. stomach muscles.
mx. first maxilla.
mx$^{i.}$ second ,,
mxp. first maxillipede.
mxp$^{i.}$ second ,,
n. nerves.
nc. nucleus.
o. ovary.
od. oviduct.
œ. œsophagus.
og. optic lobe.

om. muscles of the oviduct.
os. ovisacs.
ov. ova.
p^{i}. first pair of feet.
p^{ii}. second ,,
p^{iii}. third ,,
p^{iv}. fourth ,,
p^{v}. fifth ,,
pg. pigment.
R. right.
r. rostrum.
rep. receptaculum seminis.
rt. rectum.
rtn. retina.
ry. fin ray.
S. spermatozoa.
sbg. subœsophageal ganglion.
sf. sternal fork.
sg. cement gland.
sp. spermatophore.
spg. supra-œsophageal ganglion.
st. stomach.
t. testis.
V. ventral.
va. vagina.
vd. vas deferens.
vu. vulva.
y. opening of digestive duct into the stomach.
z. pore canals.

Nos. 1 to 13 nerves, as follows:—
1. optic.
2. antennules.
3. antennæ.
4. mandibles.
4a. lateral frontal margins.
4b. first maxillæ.
5. second maxillæ.
5a. lateral cephalic muscles.
6. first maxillipedes.
7. second maxillipedes.
8. first feet.
8a. stomach muscles.
9. second feet.
9a. posterior cephalic muscles.
10. third feet.
11. fourth feet.
12. abdomen.
13. fifth feet.

Plate I.

Fig. 1. *Lepeophtheirus pectoralis*, mature female, dorsal view. × 17.

Fig. 2. *Lepeophtheirus pectoralis*, mature male, dorsal view. × 17.

Fig. 3. *Lepeophtheirus pectoralis*, nauplius stage, newly hatched. × 52.

Fig. 4. *Lepeophtheirus pectoralis,* "chalimus" stage. × 26.

Fig. 5. *Caligus rapax,* early "chalimus" stage attached to fin ray of young cod, the line *d' e'* represents the surface of the skin. × 54·4.

Fig. 6. *Caligus rapax,* "chalimus" stage, previous to throwing off the filament attachment. On tail of young lumpsucker. × 15·24.

Fig. 7. *Caligus rapax,* mature, part of the frontal plate showing a lateral sucker. × 22.

Plate II.

Lepeophtheirus pectoralis.

Fig. 1. Female, ventral view, showing the various appendages and their muscles. × 17.

Fig. 2. Female, dorsal view, showing the chief muscles and blood currents. The arrows indicate the course of the blood. × 17.

Fig. 3. Female, ventral view, showing the digestive gland, its duct and alimentary canal. × 17.

Fig. 4. Female, ventral view, showing the reproductive organs. × 17.

Fig. 5. Male, ventral view, showing the reproductive organs. × 26.

Fig. 6. Genital segment and abdomen of an immature female, ventral view, showing vulva (*vu.*). × 40.

Fig. 7. Spermatophores detached from genital openings of a female. × 25.

Fig. 8. Mouth from the anterior base, with the mandibles inside, showing the muscles and ducts of digestive gland. × 25.

Fig. 9. Digestive gland. × 77.

Fig. 10. Longitudinal section of the ovary. × 50.

Fig. 11. Transverse section of pore-canal at the base of the mouth. × 350.

Plate III.

Lepeophtheirus pectoralis.

Fig. 1. Female, ventral view, showing the nervous system *in situ.* × 17.

Fig. 2. The nervous system from the ventral aspect. × 38.

Fig. 3. Female, nearly median longitudinal section. × 17.

Fig. 4. One of the antennules, showing the nerve endings. × 76.

Fig. 5. Median longitudinal section of the ganglia, showing the "pinhole" œsophagus passing through between the supra and sub-œsophageal parts. × 77.

Fig. 6. Transverse section in the region of the eyes. × 38.

Fig. 7. Transverse section in the region of the supra- and sub-œsophageal ganglia. × 35.

Fig. 8. Transverse section in the region of the second maxillipedes. × 30.

Fig. 9. Transverse section through the genital segment, female. × 30.

Fig. 10. Transverse section through the genital segment, male. × 38.

Fig. 11. Part of a transverse section of the intestine. × 76.

Fig. 12. Horizontal section of the dorsal aspect of the supra-œsophageal ganglion, showing the crossing of the fibres of the optic nerves. × 152.

Fig. 13. Transverse section of the eyes. × 152.

Plate IV.

Lernæa branchialis.

Fig. 1. Mature female, from the right side. The line $f' \; g'$ shows how much of the anterior portion is buried in the branchial arch. × 4·3.

Fig. 2. Nauplius stage, newly hatched. × 50·8.

Fig. 3. Very young female, unfertilised, dorsal view. From gills of flounder. × 51·5.

Fig. 4. Fertilised female, dorsal view. Just after leaving the gills of flounder. × 27·6.

Fig. 5. Mature male, dorsal view. From gills of flounder. × 28·5.

Fig. 6. Fertilised female, "Penella" stage, dorsal view. Just after settling on gills of *Gadus* (whiting). × 15·5.

Fig. 7. Later stage than Fig. 6, from the left side. The folding has just finished. Nat. size.

Fig. 8. Apex of gill filament of flounder, showing malformation caused by the young *Lernæa.* × 18·6.

Fig. 9. Apex of gill filament of flounder, normal. × 18·6.

Plate V.

Lernæa branchialis.

Fig. 1. Fertilised female, ventral view, showing the appendages, the reproductive organs, and nervous system. × 47·6.

Fig. 2. Nearly median longitudinal section of the same. × 47·6.

Fig. 3. Transverse section in the region of the eyes. × 80.

Fig. 4. Mature female, from the right side, showing the first maxillipede and the four pairs of feet, the alimentary canal and the reproductive

organs. The specimen was cleared in xylol, and the right anchor process removed. × 4.

Fig. 5. Transverse section through α β, (Fig. 4,) showing the muscular wall, the ovary, oviduct, cement gland, and intestine. × 9.

Fig. 6. Transverse section through x β, (Fig. 4,) just anterior to the rectum. × 20.

Fig. 7. Portion of the cement gland. × 20.

Fig. 8. Front view of the anchor processes of an adult female. × 4.

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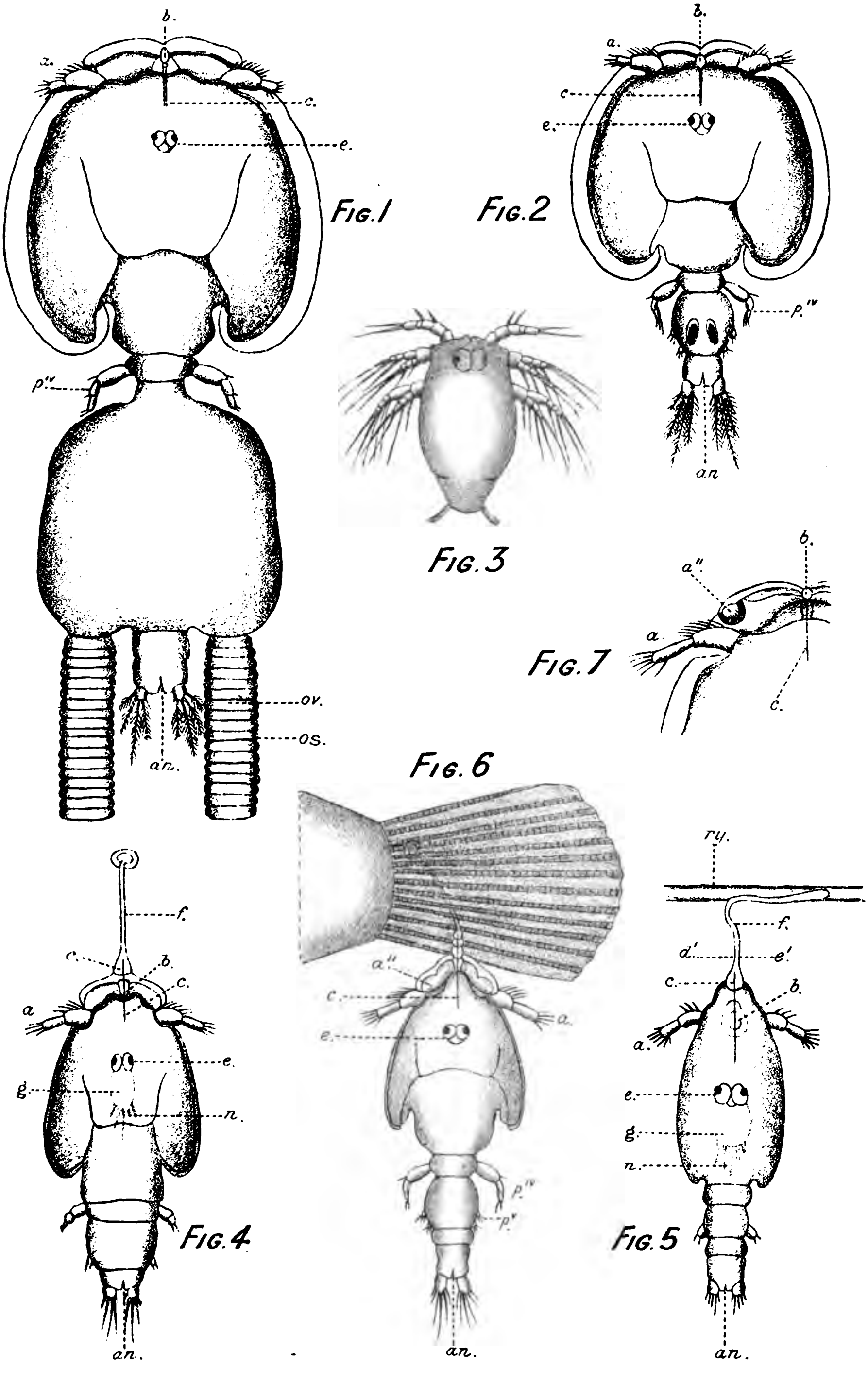
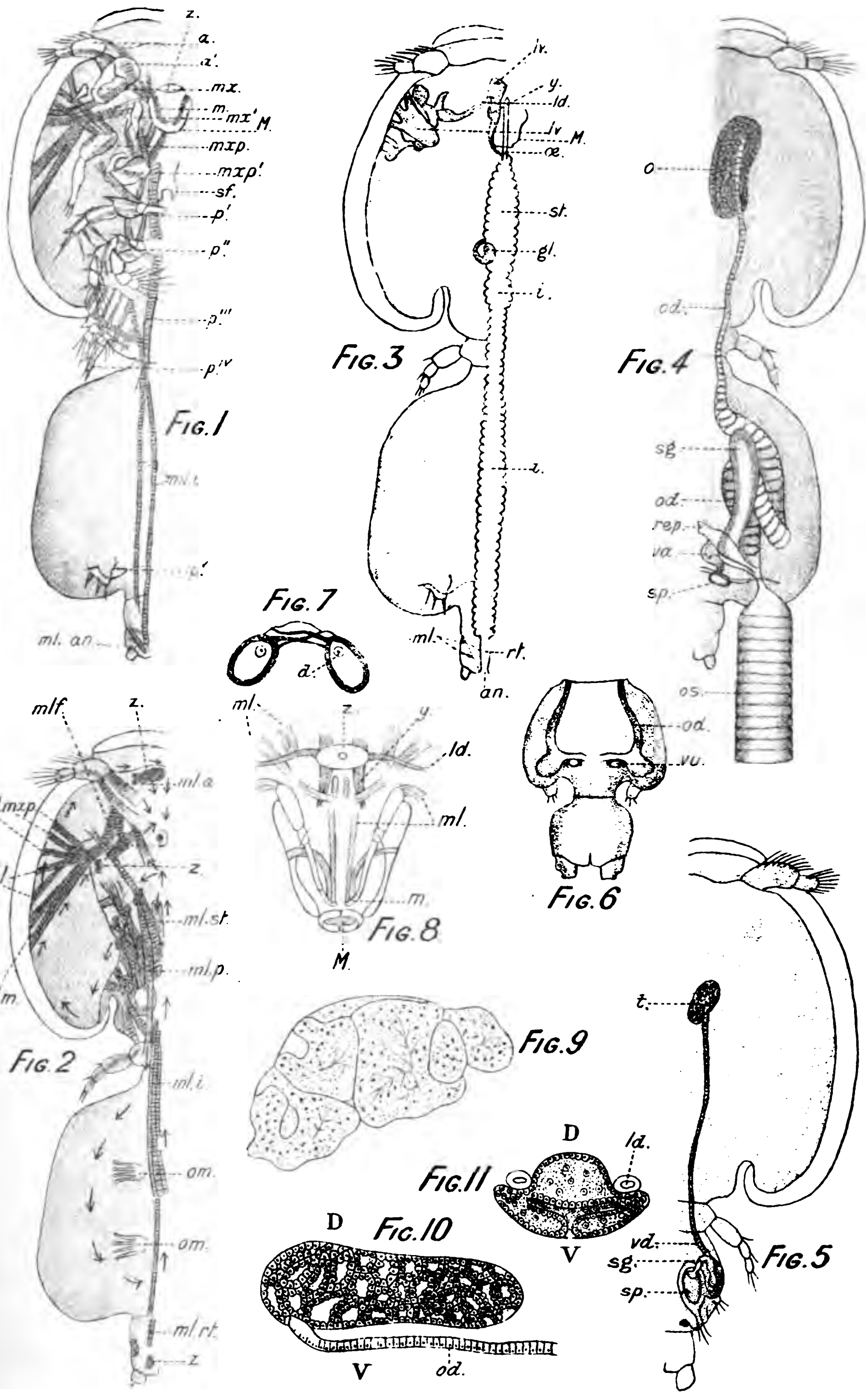


A. Scott, del. S.B. lith.

LEPEOPHTHEIRUS & LERNÆA.



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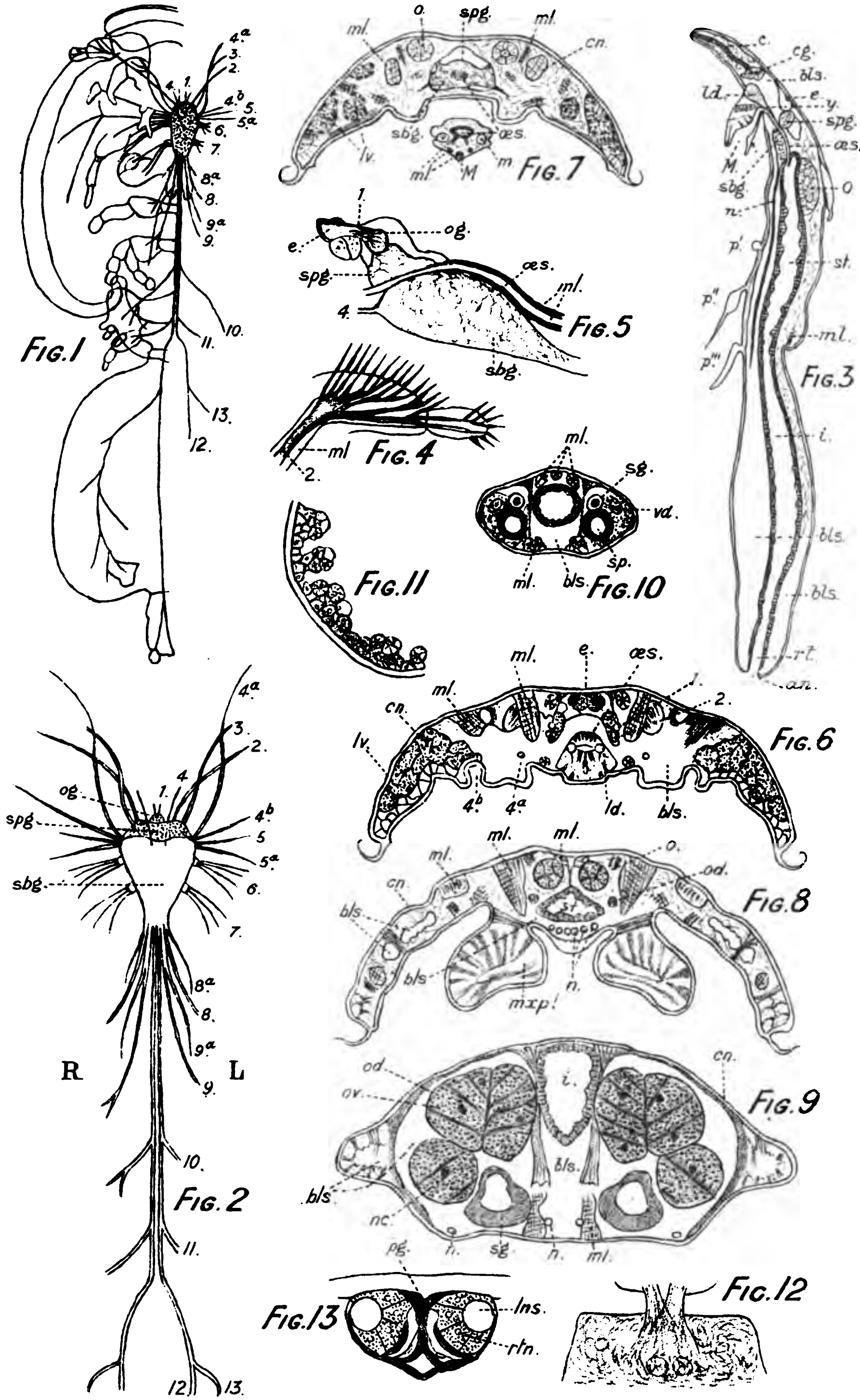
LEPEOPHTHEIRUS & LERNÆA.



A. Scott, del. S.B. lith.

LEPEOPHTHEIRUS & LERNÆA.